



INFLUENCE OF SPRING TEMPERATURES AND INDIVIDUAL TRAITS ON REPRODUCTIVE TIMING AND SUCCESS IN A MIGRATORY WOODPECKER

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ABSTRACT.—We investigated the effect of spring temperatures, female age, and female body condition on the timing of laying in a migratory woodpecker, the Northern Flicker (*Colaptes auratus*), and looked at the relationship between laying date and reproductive success. Average annual laying dates in the population, recorded over 12 years, were not related to the North Atlantic Oscillation or the Pacific–North American climate indices but were earlier when average daily temperatures along the migration route of Northern Flickers along the Pacific coast of North America were warmer. However, the strongest negative correlation between laying dates and ambient temperatures occurred after the arrival of most birds on the breeding site, which suggests that the ability of females to accumulate resources for egg laying on the breeding site was an important determinant of laying times. At the population level, egg laying advanced by 1.15 days for every degree warmer on the breeding grounds. At the level of individuals, laying dates advanced as females aged from 1 to 3 years, and females in better body condition also laid earlier. However, there was no interaction between female age and ambient temperature, which suggests that the age classes had equal capacity to respond to environmental change. Reproductive output declined seasonally as a result of declines in clutch size and not as a result of reduced fledging success. This suggests that there is no ecological mismatch linked to prey availability for Northern Flickers and that individuals could benefit by laying earlier if spring temperatures allow. *Received 3 February 2010, accepted 11 July 2010.*

Key words: climate, clutch size, *Colaptes auratus*, fledging success, laying date, migration, Northern Flicker, woodpecker.

Influencia de las Temperaturas de Primavera y de Rasgos de los Individuos sobre el Momento y Éxito de la Reproducción en un Pájaro Carpintero Migratorio

RESUMEN.—Investigamos el efecto de las temperaturas de primavera, de la edad de las hembras y de su condición corporal sobre el momento en que pone los huevos un pájaro carpintero migratorio, *Colaptes auratus*, y examinamos la relación entre la fecha de postura y el éxito reproductivo. El promedio anual de la fecha de postura, registrado durante 12 años, no estuvo relacionado con la oscilación del Atlántico Norte ni con los índices climáticos del Pacífico norteamericano, pero la fecha de postura fue más temprana cuando las temperaturas diarias a lo largo de la ruta de migración de *C. auratus* en la costa Pacífica de América del Norte fueron mayores. Sin embargo, la correlación negativa más fuerte entre las fechas de postura y las temperaturas ambientales se presentó después del arribo de la mayoría de las aves a sus sitios de cría, lo que sugiere que la habilidad de las hembras para acumular recursos para la postura de huevos en el sitio de cría fue un determinante importante de las fechas de postura. A nivel de la población, la postura se adelantó en 1.15 días por cada grado de aumento en la temperatura de las áreas de cría. A nivel de los individuos, las fechas de postura se adelantaron a medida que las hembras envejecieron de 1 a 3 años. Además, las hembras en mejor condición corporal pusieron más temprano. Sin embargo, no existió interacción entre la edad de las hembras y la temperatura del ambiente, lo que sugiere que las clases de edad presentaron la misma capacidad de responder al cambio ambiental. El rendimiento reproductivo disminuyó estacionalmente como resultado de disminuciones en el tamaño de la nidada y no de una reducción en el éxito de emplumamiento. Esto sugiere que no existe un desacople ecológico ligado a la disponibilidad de presas para *C. auratus* y que los individuos se podrían beneficiar de poner más temprano si las temperaturas de primavera lo permiten.

THE URGENT NEED to study the effects of changing climates on organisms has motivated many recent studies on the effect of abiotic cues on the timing of breeding. Analyses of long-term data collected over decades for several avian species have revealed shifts to earlier mean laying dates concurrent with warmer springs (reviews in Dunn 2004, Lehtikoinen et al. 2004). Among the possible

explanations for the advancement of laying dates in migratory birds is that migration is accelerated so that birds arrive on the breeding grounds earlier (Huin and Sparks 2000, Marra et al. 2005). However, little information is available about how climate or weather interacts at different scales to influence reproductive timing. For example, a population of Pied Flycatchers (*Ficedula*

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hypoleuca) increased migration rates in response to higher temperatures along their flyway but did not advance laying because local phenology did not advance (Ahola et al. 2004). Thus, there may be different effects of weather on the wintering grounds, along the migration route, and locally at the breeding site, but the relevant period over which to quantify weather is often unknown (Gordo and Sanz 2008).

Modeling how breeding parameters are related to variation in spring weather is key to predicting future effects on a population associated with changing climate (Martin and Wiebe 2004). Predicting a population's response to climate change also requires an understanding of how traits of individuals may interact with abiotic conditions to determine reproductive timing (Benton et al. 2006, Wilson et al. 2007). For example, high-quality individuals may be buffered from harsh climatic conditions and, thus, be able to accumulate body reserves more quickly and lay relatively earlier than younger or lower-quality individuals. Theory suggests that age-related differences in reproductive performance should be greater in harsher environmental conditions (Martin and Wiebe 2004), but few studies have attempted to incorporate both weather and individual traits to explain variation in laying dates (Pulido 2007, Visser et al. 2009) or explicitly test for differential effects on age classes within a population (Wilson et al. 2007, Nevoux et al. 2008).

Ultimately, it is crucial to measure the reproductive success of individuals with different reproductive timing to predict fitness consequences. An early onset of breeding in birds has been viewed traditionally as a beneficial trait that allows access to the most food or production of the most clutches in a season (Lack 1968, Drent and Daan 1980). Recently, others have emphasized that it may be more important to adjust reproductive timing precisely to seasonal prey abundance. According to the "ecological mismatch hypothesis" (Visser et al. 1998), climate change causes a shift in the timing of peak prey abundance in relation to the timing of egg laying, resulting in poor fledging success. The mismatch hypothesis has garnered much recent attention and some support among passerines with insect or larval prey such as Great Tits (*Parus major*) and Pied Flycatchers (Sanz et al. 2003, Visser et al. 2004). However, other birds with different diets or life histories may be tolerant of, or even benefit from, advancing spring phenology. Therefore, it is important to determine which mechanisms drive reproductive output for a variety of species, and the time during the breeding cycle when weather has the greatest effect on fitness.

Most studies on climate and the timing of egg laying have focused on insectivorous passerines (Møller et al. 2004) or seabirds (e.g., Barbraud and Weimerskirch 2006, Reed et al. 2009), so there is a great need for information from other avian taxa. Woodpeckers feed on insects but rely on prey types that have different life histories and so provide useful ecological contrasts. Here, we focus on the causes and consequences of reproductive timing in the Northern Flicker (*Colaptes auratus*; hereafter "flicker"), a common North American woodpecker and a short-distance migrant. The main prey of flickers, ground-dwelling ants (Wiebe and Moore 2008), do not have as short or as sharp a peak in abundance as the lepidopteran larval prey that have been the focus of other avian studies (Azcarate et al. 2007, Dunn et al. 2007). Hence, we predicted that fledging success of flickers would be relatively insensitive to laying date. Our main goals were to (1) determine when and where temperatures along the migration route are associated with

laying dates in the population, (2) examine the role of environmental factors (spring weather) together with individual factors (age and body condition) in predicting reproductive timing of individual females and to see whether there were differential effects for different age classes, and (3) examine the effect of laying date on an individual's reproductive success.

METHODS

Study site and study species.—Field work was carried out at Riske Creek, British Columbia (51°52'N, 122°21'W), where 100–165 flicker nests have been monitored annually on an area of about 75 km² from 1998 to 2009. For a detailed description of the habitat and nest trees, see Aitken et al. (2002). Flickers here are short-distance migrants that remain north of the tropics; band recoveries show that individuals in the population winter west of the Rocky Mountains, along the Pacific coast, from southern British Columbia to central California in the Sacramento Valley (Flockhart and Wiebe 2007). Most pairs arrive on the study area in spring during the last 2 weeks of April, but we are unable to record exact arrival dates of breeders because many are unbanded recruits. We use tape-recorded territorial calls in spring to locate active territories and check potential cavities using flashlights and mirrors every 2 or 3 days until eggs are found. During laying, small, replaceable access doors are cut into the tree trunks, which does not disturb breeding (Fisher and Wiebe 2006) but gives access to nestlings and adults for banding. Laying dates, clutch size, hatching success, and nestling mortality are documented for all breeding pairs by checking nests every 4 or 5 days.

Annually, >95% of known breeding adults on the study area were trapped at the nest either by stuffing the nest hole during incubation or by pulling a net over the cavity entrance during brood rearing. Birds were weighed, measured, and aged up to 4 years according to molt patterns described in Pyle (1997). The body mass of adults tends to drop after nestlings are ~1 week old but is fairly stable before then (K. L. Wiebe unpubl. data), so we used only measurements of body mass obtained before that date. For a multivariate measure of body size (Rising and Somers 1989), we used the score on the first axis of a principal component analysis (PC1) based on six measures: lengths of the wing, bill, tail, tarsus, ninth primary, and bill depth (see Wiebe 2000). For an index of nutrient reserves, we regressed body mass against PC1 to control for structural size and used the residuals as a measure of body condition.

Weather data.—Some studies have linked the timing of migration in birds with large-scale climate phenomena such as the North Atlantic Oscillation (NAO) and the Pacific–North American (PNA) index (Forchhammer et al. 1998, Hüppop and Hüppop 2003). The NAO is an atmospheric circulation index linked to interannual variations of the winter climate in eastern North America (Hurrell 1995), whereas the Pacific Oscillation may influence climate patterns along the Pacific west coast. Monthly indices for NAO and PNA are standardized for 3-month periods (i.e., March patterns are calculated on the basis of February through April mean monthly standardized anomaly fields; National Weather Service Climate Prediction Center [see Acknowledgments]). Thus, we correlated annual laying dates in the population with the March and April index values that most likely corresponded to late-wintering and early-migration times in our flicker population.

We also examined the effect of temperature during migration at a finer geographic scale, along the probable migration route of flickers, by obtaining data from five weather stations: Sacramento, California; Eugene, Oregon; Seattle, Washington; Vancouver, British Columbia; and Williams Lake, British Columbia (data retrieved online from the [U.S.] National Weather Service and Environment Canada). A sliding time-window approach (Slagsvold 1976, Ahola et al. 2004) was used to determine the period that was most closely correlated with annual average laying dates in the population. Ahola et al. (2004), who studied long-distance migrants, used a 3-week time window, but we used a shifting time window of a 2-week block for a finer-resolution time scale, which is probably more appropriate for a short-distance migrant such as the flicker, and we advanced the time-window in 3-day intervals. We used this approach on weather data (mean daily temperatures) from each of the five locations, starting from the 2-week period of 2–15 March and ending with 18–31 May, just after the average mean laying date in the population.

Data from a weather station on our study site at Riske Creek were only available until 2002, so we used temperatures from the nearest weather station at Williams Lake, which is 32 km away. Daily temperatures within the four summer months (April–July) were strongly correlated between Riske Creek and Williams Lake (all $r^2 > 0.9$, $P < 0.001$) and differed by only a small absolute amount (0.40–0.55°C; paired t -test, all $P > 0.04$). Therefore, we assumed that temperatures from Williams Lake accurately reflected local temperatures on our study site.

Modeling laying date and reproductive performance.—We combined abiotic weather conditions with individual attributes (age and body condition of female) in an analysis of covariance (ANCOVA) model to examine sources of variation in the reproductive timing of individual females. Laying dates of the first egg were normally distributed, so we used parametric models (general linear models [GLM]). We used only the first nesting attempt of the season for each female in the first recorded year of breeding on our study area, thus excluding data on the same female in multiple years. Age of the female was categorized as 1, 2, or 3+ years and was treated as a fixed factor, whereas body-condition residuals were entered as covariates in the model. We included two types of temperatures as covariates in the models, as in Pryzbylo et al. (2000) and Potti (2008). The first temperature variable was designed to represent conditions on the study area after migration but before egg laying (i.e., the time during which females may be accumulating nutrient reserves for egg laying). For this, we calculated the average daily temperature from the 15 days spanning 20 April to 4 May each year.

As a second temperature variable, we calculated for each female the mean daily temperature on the fifth day before its first egg. Rapid yolk deposition is initiated in the follicle ~4 days before laying in small Blue Tits (*Cyanistes caeruleus*; Kluyver 1952) and ~5 days before laying in larger European Starlings (*Sturnus vulgaris*; Ricklefs 1974), so temperatures on these days could be a proximate cue to trigger the start of the laying process. However, a preliminary analysis showed a significant positive correlation between the average daily temperature 5 days before laying (prelaying temperature, PLT) and the laying date ($r^2 = 0.07$, $P < 0.0001$) simply because ambient temperatures warmed up as the season progressed on our study area. Therefore, we also calculated a PLT residual, which was the difference between the PLT and the

“expected” temperature for that date based on historical 30-year averages from the weather station at Williams Lake. The PLT residuals were not correlated with date ($r^2 = 0.003$, $P = 0.13$). Nevertheless, we expected that PLT residuals would have a differential effect on triggering follicular development, depending on the actual ambient temperature (e.g., a day that is 5°C warmer than the long-term average should have a relatively stronger effect earlier in the season, when ambient temperatures are cold, than later in the season, when all temperatures are warm). To control for this in the model, we included both PLT (absolute temperature) and PLT residuals (temperature in relation to the long-term average), along with an interaction term between them in all the models. To test the hypothesis that females of different ages reacted differently to spring weather conditions, we also included an interaction term between age and spring temperature in the final model. Initially, we ran models containing all other possible second-order interactions, but none of these were significant (all $P > 0.35$), so they were not retained in the final model.

Clutch size (range: 2–14) and the number of fledglings followed a normal distribution, so we used parametric GLM (ANCOVA) models in SPSS, version 17.0 (SPSS, Chicago, Illinois), and initially included all possible second-order interaction terms (as above). Fledging success, or the proportion of the brood to fledge (number of fledglings/clutch size) was arcsine transformed to obtain a normal distribution. If food supply has a sharp peak during the nestling period, fledging success (i.e., inverse of nestling mortality) and fledgling production should also follow a peak over the season (Visser et al. 2006). However, different spring phenology in different years means that the date of the peak could vary annually, so relationships between reproductive success and date must be calculated separately for each year. Thus, we modeled (1) a linear relationship and (2) a quadratic (peaked) relationship for each year separately and then for all years pooled.

RESULTS

Effects of climate at the population level.—We recorded the dates of the first egg for 1,182 first clutches and with the 12 years pooled; the earliest laying date was 26 April, and the mean was 14 May (± 7.68 days [SD]). Annual mean laying dates in the population varied from 10 to 18 May (i.e., over a span of 8 days; Fig. 1). Over the 12 years, we could not detect a directional increase in monthly average temperature on the study area for either April (regression: $r = 0.24$, $P = 0.443$) or May ($r = 0.04$, $P = 0.91$). Likewise, there was no significant relationship between year and mean laying date, which indicates that there was no directional temporal trend for earlier dates ($r = 0.09$, $P = 0.76$; Fig. 1). Between 1998 and 2009, the annual mean laying date of first clutches was not correlated with the NAO index for March ($r = 0.02$, $P = 0.77$) or April ($r = 0.22$, $P = 0.49$); nor were laying dates correlated with the PNA index (March: $r = 0.35$, $P = 0.27$; April: $r = 0.45$, $P = 0.14$).

On a finer geographic scale, the sliding time-window approach indicated that spring temperatures at the five cities along the migration route were generally negatively correlated with laying dates; higher temperatures were associated with earlier dates. The best correlations ($r = -0.78$ to -0.82) were found for the 2-week blocks starting around Julian dates 115–121 (i.e., 25 April–1 May; Fig. 2). These dates corresponded to the 1 to 2 weeks before laying

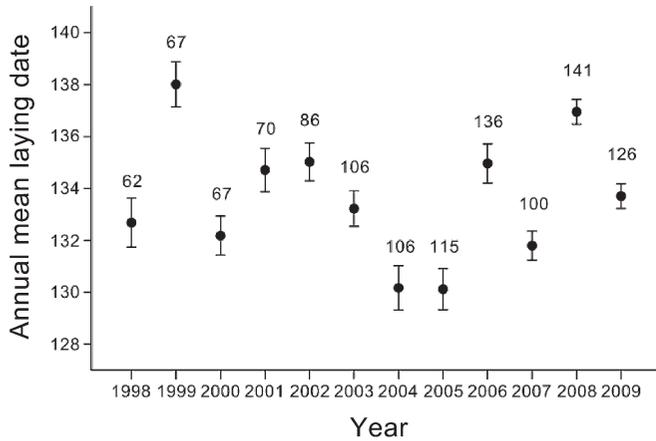


FIG. 1. Average laying dates (Julian dates \pm SE) within a population of Northern Flickers in central British Columbia, Canada, over a period of 12 years. Only first clutches are shown, with sample sizes above the bars. Julian date 128 = 8 May.

for most birds in the population (see above: overall mean laying date = 14 May). During this period, temperatures in Sacramento, the most southerly wintering location, showed the weakest correlation with laying times, whereas temperatures at the three northern locations (Williams Lake, Vancouver, and Seattle) had similar and high correlations. However, earlier in spring, during the 2 weeks beginning from Julian date 63 (4 March), temperatures in Sacramento were, of all the cities, most strongly correlated with laying dates and also fairly strongly ($r = -0.76$; Fig. 2).

Determinants of individuals' laying dates.—Both of the biotic factors in the ANCOVA were significant predictors of laying dates (Table 1). Older females laid earlier in the season, with laying dates advancing by ~ 3 days between ages 1 and 2 years (Bonferroni post hoc test: $P < 0.001$) and by ~ 1.5 days between 2 and 3+ years of age (Bonferroni $P = 0.04$; Fig. 3). Females in better body condition also laid eggs sooner (regression slope = -0.12). There was no

TABLE 1. Results of an ANCOVA explaining the variation in laying dates of female Northern Flickers. Only first nesting attempts of the year and only one observation per female are included, and data from 1998 to 2009 are pooled. Spring temperature is the average daily temperature during 15 April–4 May each year. Prelaying temperature (PLT) is the average daily temperature 5 days before a female's laying date. PLT residuals are the difference between the long-term average "expected" temperature for the study area on that date and the PLT. Females were categorized into three age classes (see text).

Factor	Type	df	F	P
Female age	Fixed factor	2	16.5	0.001
Female condition	Covariate	1	7.3	0.007
Annual mean spring temperature	Covariate	1	48.5	0.001
PLT	Covariate	1	690.0	0.001
PLT residual	Covariate	1	262.0	0.001
PLT*PLT residual		1	2.08	0.14
Age*spring temperature		2	0.16	0.84
Error		846		

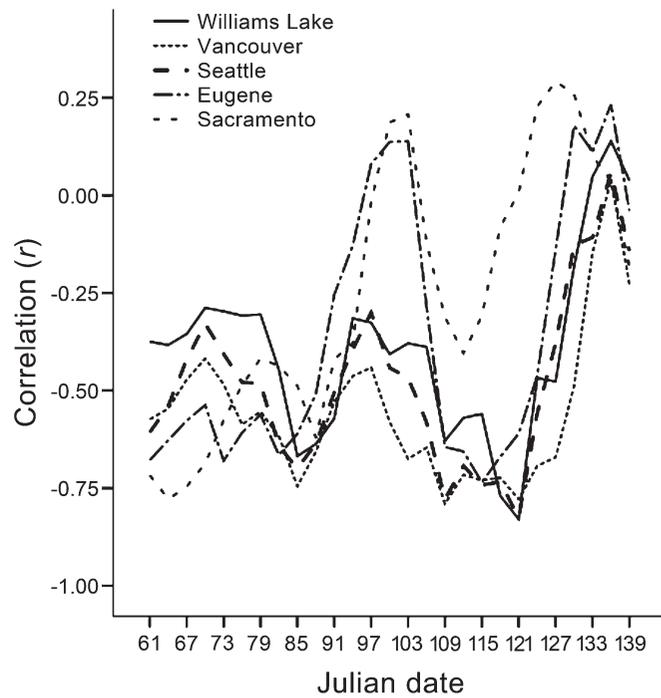


FIG. 2. Correlations between annual mean laying dates in the population and average daily spring temperatures at five cities along the migration route of Northern Flickers. Temperatures were calculated as the mean for a 2-week block beginning on the Julian date shown (61 = 2 March), and the time frame was moved forward in 3-day intervals.

interaction between female age and spring temperatures, which indicates that differences among age classes persisted regardless of temperature regimes. Average daily temperature on the study area during the 2 weeks after arrival varied considerably, from

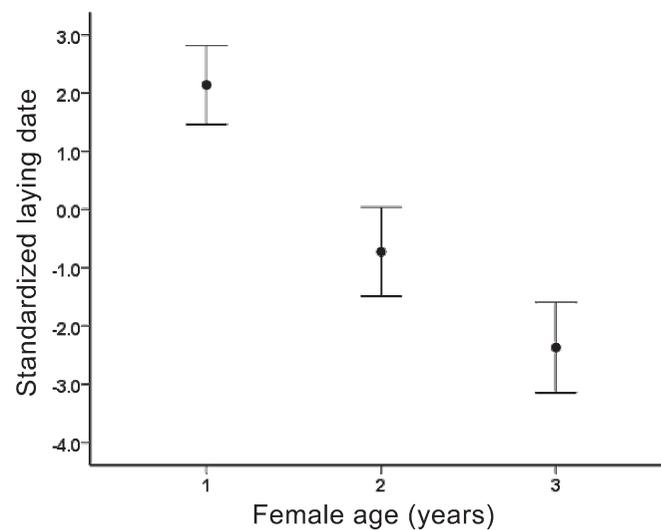


FIG. 3. Mean standardized laying dates (\pm SE) for female Northern Flickers from the first year of life to ≥ 3 years of age. Laying dates within each year were standardized by subtracting from the population mean.

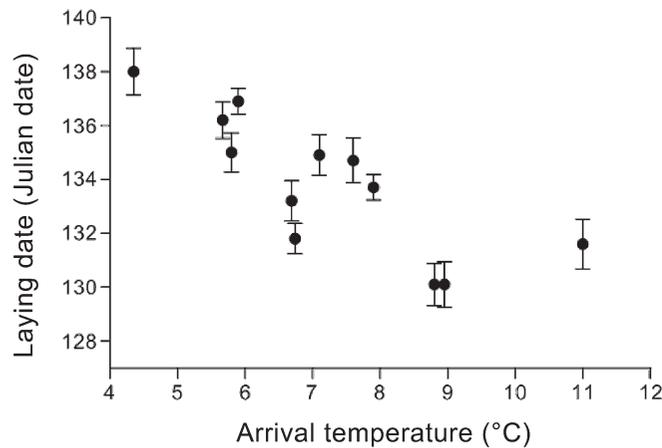


FIG. 4. Average laying dates of first clutches of Northern Flickers at Riske Creek, British Columbia. Laying in the population became earlier as average daily temperature in a 2-week block spanning 24 April–7 May increased. This represents the time just after arrival of most individuals after migration and before most clutches are initiated.

about 4°C to 11°C over the 12 years of the study (Fig. 4), and was also negatively associated with laying dates (Table 1). The slope of a linear regression through these average annual laying dates was $-1.15 \text{ days } ^\circ\text{C}^{-1}$, but visual inspection suggests a threshold around 9°C where laying date did not advance further. As expected, there was a significant interaction between the absolute temperature on the day 5 days before a female laid her first egg (PLT) and the temperature residual on that day (Table 1). A partial correlation controlling for PLT revealed a negative relationship between PTL residuals and laying date ($r = -0.65$, $P < 0.001$; i.e., unusually high temperatures 5 days before laying were associated with earlier laying dates, especially when the ambient temperature was cool).

Effect of laying date on reproduction.—Among first nesting attempts for all 12 years pooled, clutch size declined with laying date (ANCOVA: $F = 228$, $df = 1$ and $1,052$, $P < 0.001$) and was associated with the random factor year ($F = 1.86$, $df = 11$ and $1,052$, $P = 0.04$), but there was no interaction between year and the slope of the decline in clutch size ($F = 1.57$, $df = 11$ and $1,052$, $P = 0.11$). With the years pooled, clutch size declined by $0.07 \text{ eggs day}^{-1}$. An ANCOVA for second (replacement) clutches revealed a similar pattern, with the number of eggs declining with date ($F = 29.9$, $df = 1$ and 143 , $P < 0.001$), but the slope of the decline was about half as steep as that for first clutches: $0.035 \text{ eggs day}^{-1}$ (Fig. 5).

For those nests in which at least 1 offspring hatched, an average of 0.73 nestlings fledged per egg laid. The mismatch hypothesis predicts a seasonal peak in fledging success, but we found few significant relationships for either linear or quadratic relationships with date. With each year considered separately, fledging success (number of fledglings/clutch size) declined linearly with date ($P < 0.05$) in only 1 of 12 years (2008), and there was a significant quadratic relationship in only 2 of 12 years ($P = 0.015$ in 2001, when success of midseason nests was the highest, and $P = 0.04$ in 2002, when midseason nests did the poorest). With years pooled, there was no linear relationship between fledging success and laying date ($r = 0.01$, $P = 0.90$, $n = 1,034$) and no quadratic relationship ($r = 0.04$, $P = 0.23$, $n = 1,034$). Although there was no temporal pattern

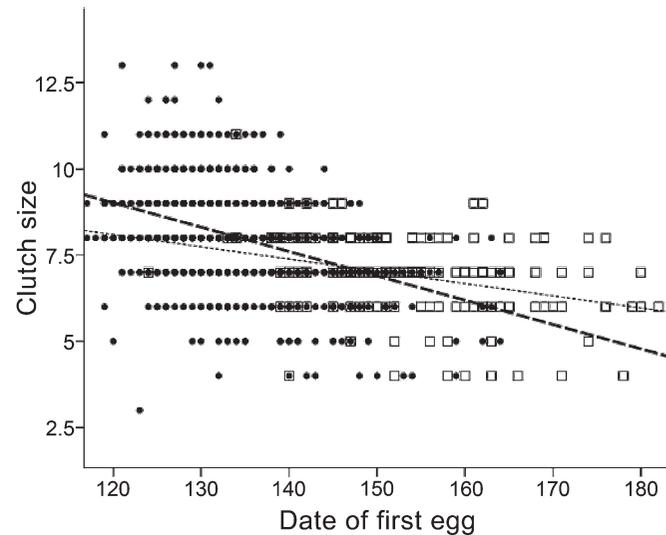


FIG. 5. Seasonal decline in clutch size of Northern Flickers for first clutches (dark circles, dashed line) and replacement (second) clutches (open squares, dotted line) at Riske Creek, British Columbia. Total sample size for all females pooled over 12 years is 1,271, but ANOVAs were calculated separately for first and second clutches.

of fledging success, the seasonal decline in clutch size meant that there was still a decline in the absolute number of fledglings produced within first clutches (ANCOVA, covariate laying date: $F = 14.4$, $df = 1$ and $1,034$, $P < 0.001$; year effect: $F = 0.69$, $df = 11$ and 994 , $P = 0.74$) and within second clutches (covariate date: $F = 4.1$, $df = 1$ and 131 , $P < 0.04$; year effect: $F = 0.69$, $df = 11$ and 131 , $P = 0.72$).

DISCUSSION

Mean atmospheric temperatures on global and continental scales have increased during the past century (Intergovernmental Panel on Climate Change 2007), but our 12-year study was probably too short to detect significant directional spring warming on our study area. Nonetheless, reproductive timing in migratory Northern Flickers was strongly correlated with temperature at a variety of spatial and temporal scales, which showed that annual productivity was influenced by weather.

Effects of temperature during migration.—At the largest geographic scale, there was no relationship between reproductive timing and the two climate indices (NAO and PNA). Previous studies that have found effects of NAO on arrival times of migrating birds have focused mainly on long-distance (tropical) migrants, so the continental scale at which the NAO and PNA climate patterns operate probably does not match very well with the smaller scale of flicker migration up the northwest Pacific coast. More relevant were the temperatures at the five cities along the migration route, and because these temperatures were somewhat correlated with each other, trends at the five locations followed a similar pattern (Fig. 2). Nevertheless, it was intriguing that in early March, the temperatures in the southernmost locations (Sacramento and Eugene) rather than the northern locations were most closely associated with laying dates, whereas this pattern reversed as spring progressed and, presumably, as flickers moved northward. Because

flickers are not yet on the breeding site in early March, this suggests that migration timing from the wintering grounds could be one factor that determines annual reproductive schedules.

Long-distance tropical migrants most likely use photoperiod rather than temperature as the major cue to begin migration (Gwinner 1996), because it is hard to predict temperatures on the distant breeding grounds from conditions on the wintering grounds. However, the rate of migration seems to be adjusted to weather, phenology, or both along migration routes in most European and North American birds (reviews in Lehikoinen et al. 2004, Marra et al. 2005). Short-distance migrants such as flickers have a better opportunity than long-distance migrants to track temperatures that reflect conditions on the breeding grounds. Because the availability of surface ants, the main food of flickers, is dependent on snow-free ground and temperatures above $\sim 5^{\circ}\text{C}$ (Azcárate et al. 2007, Dunn et al. 2007), it is not unreasonable that the northward movement of these woodpeckers is matched to (constrained by) warming temperatures along the coast in spring.

Effects of temperature at the breeding site.—Although temperature during the migratory period was related to clutch initiation dates, the strongest correlation with the average annual laying date in the population was with local temperatures at the breeding site after arrival in late April but before most egg laying (Figs. 2 and 4). The body stores of most woodpeckers do not show significant annual variation (Koenig et al. 2005), and certainly not to the extent observed in some other migratory birds such as shorebirds and waterfowl, which may increase in body mass by 100% before migration (Clark 1979). Hence, flickers probably rely more on local energy “income” for the formation of the reproductive tract and eggs than on “capital” (stored body reserves) accumulated on the wintering grounds.

Flickers lay among the smallest eggs in relation to body size of any bird (Wiebe 2006b), but this “r-selected” species invests heavily in current reproductive effort with large clutches (Wiebe 2006a), so the energetic demand on females in spring may still be substantial. Because surface ant activity is minimal below about 5°C (Azcárate et al. 2007), food for egg formation and self-maintenance could be limited in spring when daytime temperatures fluctuate around this threshold, even though the absolute amount of energy required per egg may be small (see Salvante et al. 2007). Other studies have documented direct effects of spring temperature on the availability of insect prey (Bryant 1975) and consequent proximate constraints on egg production in female birds (Perrins 1970). For example, laying dates of European Common Swifts (*Apus apus*) were negatively correlated with ambient temperature (O'Connor 1979), and Three-toed Woodpeckers (*Picoides tridactylus*) laid earlier in warmer springs, when there was an earlier development of bark beetles (Fayt 2003).

Earlier laying in years with warmer ambient temperatures is a prevalent pattern in birds; 79% of 57 studies of temperate birds reported a negative association between mean laying dates and air temperature in spring (Dunn 2004). Meijer et al. (1999) suggested that a general time window for laying is set by ambient temperatures over a period of weeks in spring and that laying within this time window is specifically triggered by a spike in temperature 5 days before the first egg is laid. Consistent with this model, female flickers generally laid earlier when the average daily temperatures spanning a period from late April to early May

were higher. Our data also suggested that rapid follicular development in flickers (and, hence, the proximate laying process) was associated with warmer-than-average temperatures occurring 5 days before the first egg was laid. Irrespective of the proximate temperature cues that may trigger egg formation, food supplementation experiments are needed to test whether the initiation of egg laying is the result of energy constraints on females at the time of laying or a strategic way to adjust reproductive investment to match predicted food availability during the nestling period (Meijer et al. 1999).

Female quality and interactions with the environment.—Female age was strongly associated with reproductive timing (Fig. 3), but there was no interaction between age and ambient spring temperatures, so older females did not do disproportionately better than younger ones in harsher spring conditions. Earlier laying with age has been reported for diverse avian taxa (Sæther 1990, Wiebe and Martin 1998), and in some cases, poor foraging skills of young birds have been implicated as the mechanism (Hipfner et al. 2003). It is possible that older females can forage more efficiently than younger ones, but given that young females did not suffer inordinately during cold weather, factors outside of physiology and foraging are probably involved. Flickers tend to pair assortatively by age and to retain the same mate if both survive (Wiebe 2005), which may save time needed for mate searching in spring (see Murphy 1996). If pairs re-form, they often reuse a former tree cavity for nesting, which can also save time and energy costs spent excavating (Wiebe et al. 2007), so old pairs could breed quickly on a home range where they are familiar with foraging areas.

Similar to the pattern in flickers, the difference in reproduction between age classes did not vary according to the severity of the weather in White-tailed Ptarmigan (*Lagopus leucurus*; Martin and Wiebe 2004) or in White Storks (*Ciconia ciconia*; Nevoux et al. 2008). By contrast, the age classes of Boreal Owls (*Aegolius funereus*) were affected differently by environmental variation because the breeding of younger, but not of older, owls was hindered in poor food years (Laaksonen et al. 2002). There is currently very little empirical data on how environmental variation may affect different age classes of bird populations differently, but this is necessary to understand population dynamics and to predict future consequences for age-structured populations (Pfister 1998).

Consequences of reproductive timing on success.—Our data suggest that average laying dates for flickers advance by 1.15 days for every degree warmer during the period just before laying (Fig. 4), although once the ambient spring temperatures reach $\sim 9^{\circ}\text{C}$, laying may no longer be constrained by temperature. This rate of advancement is within the range of 1.1–5.5 days $^{\circ}\text{C}^{-1}$ reported for 45 passerine and waterfowl species in Britain (Crick and Sparks 1999) and similar to the 1.43 days $^{\circ}\text{C}^{-1}$ reported for Mew Gulls (*Larus canus*; Brommer et al. 2008). In flickers, earlier laying increased productivity by 0.07 eggs day^{-1} and, in contrast to Pied Flycatchers, in which the decline in clutch size was steeper in warmer years (Both and Visser 2005), the rate of seasonal decline in clutch size of flickers did not vary with different temperature regimes in different years.

For species with strong seasonal declines in clutch size, and for those breeding at high latitudes with a short breeding window, the ability to respond quickly to warming spring temperatures could be a big advantage (Nolet and Drent 1998, Martin and Wiebe

2004). However, the reproductive advantages of earlier breeding seem to be species-specific and linked to whether or not ecological mismatches with food supply exist. Drever and Clark (2007) found little support for the mismatch hypothesis in ducks. Instead, they showed that laying dates advanced and nest success increased with warmer spring temperatures. Visser et al. (2004) suggested that granivores, with a food supply that is predictable from conditions at the time of laying, may be able to cope with changes in food abundance caused by climate change better than many insectivores. We emphasize that not all insect prey show the rapid peak-and-crash dynamics that lead to ecological mismatches and starvation of nestlings. Ant populations peak in summer, but gradually, such that densities are high over a period of months during the flicker's breeding season (Dunn et al. 2007). Therefore, flicker parents did not have greater difficulty feeding their offspring as the season progressed.

Initially, it appears that several woodpecker species, which depend on a variety of insect prey and use a variety of foraging techniques, are poised to profit in a scenario of climate warming, because earlier laying dates and greater productivity in warmer springs has been reported for White-backed Woodpeckers (*P. leucotos*; Hogstad and Stenberg 1997), Three-toed Woodpeckers (Fayt 2003, 2006), and Red-cockaded Woodpeckers (*P. borealis*; Schiegg et al. 2002). Similarly, flickers in central British Columbia appear to benefit from moderately warmer springs for several reasons. First, as short-distance migrants they can more easily track phenological changes on the wintering grounds and migration route that are likely to reflect conditions on the breeding site and, hence, arrive at an appropriate time. Second, their insect prey are likely to become more available earlier in spring and reduce energy constraints for females. Finally, ant prey do not show a short, sharp peak in abundance that would lead to a mismatch between supply and demand for food when nestlings are being fed. Nevertheless, Schiegg et al. (2002) and Fayt (2006) cautioned that increased fledging success does not always seem to lead to greater juvenile recruitment in woodpecker populations and so the effects of climate on juvenile dispersal and survival still require particular attention.

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